

TWO HETEROSPOROUS PLANTS
FROM THE UPPER DEVONIAN OF
NORTH AMERICA



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TWO HETEROSPOROUS PLANTS FROM THE UPPER DEVONIAN OF NORTH AMERICA

By J. M. PETTITT

I SYNOPSIS

The sporangia and spores of two heterosporous plants, *Barinophyton richardsoni* and *Archaeopteris* cf. *jacksoni* from the Upper Devonian of North America are described. The sporangial remains of the latter are compared with those of *Archaeopteris latifolia* from the Upper Devonian of Pennsylvania, and the spores of both genera are compared with Devonian dispersed spores. A reconstruction of part of a fertile branch of *Barinophyton* is presented.

II INTRODUCTION

THE plants described in this paper are compression fossils from the Upper Devonian of North America. The specimen of *Barinophyton richardsoni* from Perry, Maine, was probably collected by Sir William Dawson in the early 1860s, and the specimens of *Archaeopteris* cf. *jacksoni* were collected by W. Graham-Smith from Scaumenac Bay, Quebec, in 1937. All the specimens are in the collections of the Department of Palaeontology, British Museum (Natural History).

I should like to express my thanks to Dr. John Richardson, to Professor C. A. Arnold, to Professor H. P. Banks and especially to Dr. W. G. Chaloner for much helpful advice and discussion during the course of this work. Thanks are also due to Mr. J. V. Brown for taking some of the photographs on Plates 1 and 2.

III SYSTEMATIC DESCRIPTIONS

PTERIDOPHYTA

Genus *BARINOPHYTON* White

Barinophyton richardsoni (Dawson)

(Pl. 1, figs. 7, 8, 10 ; Pl. 2, fig. 2 ; Text-fig. 1)

DESCRIPTION. The specimen (part and counterpart) of *Barinophyton richardsoni* examined is a compression fossil consisting of poorly preserved fertile spikes or branches slightly more than 2 cm. in length which are probably incomplete.

Arising from the surface of the axis are appendages and sporangia arranged in two longitudinal rows. The spikes are lying on the bedding plane with their supposed dorsal surfaces uppermost (Pl. 1, figs. 7, 8). The arrangement of the fertile parts is very much like that described by Arnold (1939) for *Barinophyton citrulliforme* Arnold and the orientation of the specimen is based on that proposed by Arnold. The compressed sporangia and appendages form oval to elongate carbonaceous masses, about 2–3 mm. in length and 1 mm. in width, on each side of the axis. In the majority of cases adjacent sporangia on the same side of the axis are 1–2 mm. apart, but in places they are closer together forming a more or less continuous row.

Fragments of the carbonaceous material representing the sporangia were picked off with a needle and treated with Schulze's solution (nitric acid and potassium chlorate) followed by dilute ammonia. The macerated fragments were then washed

and mounted in glycerine jelly. Slight pressure with a needle on the coverslip completely disaggregated the mass and microspores and megaspores became discernible. Each of the twelve carbonaceous fragments from different regions of the fructification treated in this way yielded both microspores and megaspores. Microspores were released in large numbers; a fragment about 1 mm. square giving several hundred microspores, but only about five to ten megaspores.

Megaspores. A megaspore of *Barinophyton richardsoni* is illustrated on Pl. 2, fig. 2. The spores are usually fragmentary, and only one complete specimen has been found. They are flattened in the equatorial plane, circular to oval in outline and about 220–250 μ in greatest diameter. The triradiate mark is in the form of three simple commissures which are about 20 μ long. The exine is 2–3 μ thick and at the contact areas is darker and probably thicker than elsewhere. Most of the spores have smooth walls, but some appear to be minutely punctate.

Devonian spores with dark contact areas have been described by Lang (1931, 1932) in the sporangia of *Psilophyton* from the Lower Devonian of Gaspé (*Psilophyton princeps*) and from Scotland, but these spores are considerably smaller than the megaspores of *B. richardsoni*. Naumova (1953) has recorded two dispersed spores, *Leiotriletes nigratus* and *Leiotriletes atavus* from the Middle and Upper Devonian of the Russian Platform which have thickened contact areas, but both Naumova's spores are smaller than the *Barinophyton* megaspores. The megaspore *Trileites langi* from the Cromarty nodule beds (Achanarras horizon, Middle Old Red Sandstone) of Scotland described by Richardson (in press) is superficially similar to the megaspores of *Barinophyton* but has very much longer commissures.

Circular, trilete, thin, smooth-walled spores with short triradiate commissures and differentiated pyramic proximal areas can be included in the genus *Calamospora* Schopf, Wilson & Bentall (1944) and the inclusion of the *Barinophyton* megaspores in this genus would seem appropriate.

Microspores. Specimens flattened in the equatorial plane are more or less circular in outline and 48–62 μ in diameter. The triradiate mark is in the form of simple commissures which extend for about one-half to two-thirds of the spore radius. The outer part of the spore exine consists of a thin, highly wrinkled membrane (Pl. 1, fig. 10). In some specimens this membrane has been lost and a smooth to minutely punctate inner layer of the exine is seen. At the proximal pole, surrounding the triradiate mark of every spore, is a darker pyramic area of the exine very similar to that seen in the megaspores, but less distinct.

No dispersed spores have been described from the Devonian that exactly resemble the microspores of *B. richardsoni*. However, if found without the thin outer exinous membrane spores of this type would probably be included in the genus *Calamospora* Schopf, Wilson & Bentall.

DISCUSSION. The generally accepted interpretation of the fructification of *Barinophyton* is that of an axis having on its dorsal surface two rows of fleshy appendages, between which the sporangia are borne (Arnold 1939). The appendages are disc-shaped structures transversely oriented to the long axis of the fertile branch (Text-fig. 1).

If each carbonaceous mass between successive appendages is the remains of one sporangium as is suggested in the descriptions of this genus by Arnold (1939) and by Kräusel & Weyland (1941) it is difficult to explain the presence of both microspores and megaspores in every sporangial fragment. The possibility that the sporangia are bisexual cannot be ruled out, but it would certainly be unusual. The discovery by Arnold (1958) of both microspores and megaspores in a single sporangium of a petrified *Calamostachys* may possibly be explained by the plane of his section cutting through drooping sporangiophores on which the sporangia are obliquely arranged, and by the breakdown of the walls between a microsporangium and a megasporangium prior to fossilisation. In Arnold's pl. 10, fig. 2 the radial sporangial walls show an interruption where the microspore and megaspore masses meet; this may be the result of the plane of section passing from a microsporangium to a megasporangium at slightly different levels, rather than a bisexual sporangium. Mahabale (1956) reports sporangia containing both microspores and megaspores in living and fossil Marsileaceae, but as Pant & Shrivastava (1961 : 51, footnote) point out, Mahabale is evidently mistaking residual tapetal inclusions and abortive spores for microspores.

In *Barinophyton* the occurrence of the two types of spores together can be explained if each carbonaceous mass represents the remains of one microsporangium and one megasporangium. How these are arranged in relation to each other and to the appendage cannot be determined from the fragmentary material upon which this account is based, but appressed between the appendages as shown in Text-fig. 1 would seem the simplest explanation.

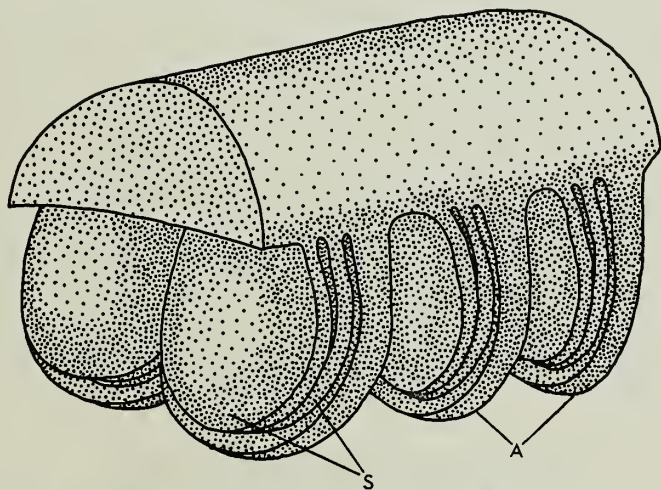


FIG. 1. Semi-diagrammatic reconstruction of part of a fertile branch of *Barinophyton* showing the possible arrangement of appendages (A) and sporangia (S). Proximal is to the right.

Ananiev (1954) described some plant remains from the Lower Devonian of Torgachino, Krasnoyarsk, U.S.S.R. as *Barinophyton obrutschevii* but later (1957)

made them the basis of a new genus *Protobarinophyton*, the organisation of the fertile parts of which is clearly similar to that of *Barinophyton*. *Protobarinophyton*, however, differs from *Barinophyton* primarily in its dichotomous mode of branching ; branching in *Barinophyton* is alternate. It is interesting to note that in his earlier account Ananiev was disinclined to attach generic importance to this character.

Kräusel & Weyland (1941) state that dichotomy of the fertile axes is known in *Barinophyton citrulliforme* and in *B. obscurum* (Dun) White from the Upper Devonian of New South Wales (Dun 1897), but in their respective descriptions of these plants none of the authors concerned (Arnold 1939, Dun 1897, White 1905) mentions this.

Perhaps some significance can be attached to the fact that *Protobarinophyton* is confined to the Lower Devonian whilst *Barinophyton* is known from the Lower, Middle and Upper Devonian. Arnold (1947) however, restricts the range to the Middle and Upper Devonian. It is tempting to assume that *Protobarinophyton* and *Barinophyton* represent stages in the phylogeny of a single line, the members of which are dichotomously branched in the Lower Devonian and become alternately branched higher in the succession. Unfortunately, nothing can be seen of the branching of the Lower Devonian *Barinophyton dawsoni* Kräusel & Weyland (1941).

Ananiev (1954, 1957) has found that the primary xylem of *P. obrutschevii* is a cylindrical protostele composed of annular tracheids and this is surrounded by homogenous parenchymatous tissue, which comprises the bulk of the axis. The anatomical structure and branching habit of the plant is therefore suggestive of a psilopsid or lycopsid form, but in the organisation of the fructification it is quite unlike these plants. Although Ananiev does not record the presence of spores in the sporangia of his new genus he was able to demonstrate that the sporangia were relatively massive organs which had a longitudinal suture for dehiscence.

The anatomy of *Barinophyton* is completely unknown and any detailed considerations as to its true affinities will have to wait until adequate material is discovered.

Arnold (1939) has reported the occurrence of smooth-walled spores, 300–400 μ in diameter, in carbonaceous remains of the sporangia of *Barinophyton citrulliforme* from the Upper Devonian of Cattaraugus County, New York, which he later (1947) judges to be megaspores. Kräusel & Weyland (1941) observed an indistinct row of four to five circular bodies, 0.1 to 0.2 mm. in diameter and of uncertain nature, on the fertile branches of *B. dawsoni*. Those authors suggest that these bodies might be either sporangia or large spores.

The present account of microspores and megaspores in *B. richardsoni* supports Arnold's conclusion that *Barinophyton* is heterosporous.

PROGYMNOSPERMOPSIDA Beck

ARCHAEOPTERIS Dawson

Archaeopteris cf. *jacksoni* (Dawson)

(Pl. 1, figs. 1–6, 9 ; Pl. 2, fig. 1)

Arnold (1936) describes and illustrates fertile pinnae of *Archaeopteris* from Scaumenac Bay, Quebec, as probably referable to *Archaeopteris jacksoni*. The

fertile pinnae from the Escuminac formation of the same locality which I have examined resemble Arnold's material so closely that I consider that they probably belong to the same species.

Two of the specimens (V.51312, V.51316) from which spores were obtained are fragments of fertile pinnae (Pl. 1, figs. 2, 3), one consisting of the distal ends of two pinnae about 2 cm. long, the other of four pinnae about 2.5 to 3 cm. long. The pinnae on each specimen are so arranged that they have obviously been part of a parallel series on the same leaf. The third specimen (V.44711) is a large fertile primary pinna, 24 cm. long and bearing 18 or 19 pinnae (Pl. 1, fig. 1). The smaller specimens are preserved in a very soft sandstone from which the entire spore-masses could be dissected out with a needle. The third, more complete specimen is preserved in a much more indurated, finer grained sandstone and the remains of the sporangia were removed from this with cellulose nitrate film pulls. When dissected out the spore-masses were treated with hydrofluoric acid to remove any adherent mineral matter, individually macerated in Schulze's solution followed by dilute ammonia and mounted in glycerine jelly, Canada Balsam or "Clearcol". The cellulose nitrate film pulls when removed were treated with dilute hydrofluoric acid, washed and dried, and mounted in Canada Balsam.

In the two smaller specimens, from which the most complete sporangial remains were obtained, the sporangia are represented only by spore-masses; no remnant of the sporangium wall cuticle has been preserved. The macerated spore-masses are of two kinds, both usually 0.3 to 0.5 mm. wide, but some 1.7 to 2.8 mm. long consisting of several hundred microspores 45–70 μ in diameter and others 1.2 to 2.6 mm. long of 9–48 (usually about 15–25) megaspores 110–370 μ in diameter (Pl. 1, figs. 5, 6). By teasing the spore-masses with a pair of needles the spores were separated.

Megaspores. The megaspores of *Archaeopteris* cf. *jacksoni* when flattened in the equatorial plane are more or less circular in outline. The triradiate mark extends between one to two-thirds of the spore radius and is either in the form of simple commissures or laesurae with labra (lips) about 5 μ wide. A conspicuous inner membrane (mesosporium?) can be seen in some spores. Paraffin sections of the megaspore-masses (for embedding and sectioning technique see Chaloner & Pettitt 1964) cut at intervals of 6 μ show that the spore exine is composed of two distinct layers; an inner homogenous layer about 2 μ thick is surrounded by a granular layer 6–7 μ in thickness. The exine sculpture of the spores is somewhat variable. In some specimens the entire spore coat is evenly covered with minute rounded to conical projections (coni) 1–2 μ high and 1 μ broad at the base (Pl. 2, fig. 1), whilst in others it is unevenly covered either with elements that are more or less circular in radial projection and about 1 μ or less in height (grana) or with elements in which the height (1–2 μ) is greater than the basal diameter and in which the upper end is not much broader than the base (baculae). In some spores the sculptural elements on the contact areas are rather smaller than those covering the rest of the exine, and in others the distal limits of the contact areas are marked by weak curvaturae formed by coalescent sculptural elements.

Megaspores with a mesosporium and a uniform decoration of coni can be included

in the genus *Biharisporites* Potonié (1956), and clearly some of the *Archaeopteris* megaspores could also be included in this genus. However, the variation in exine sculpture of some of the spores makes it difficult to assign them to a single genus based purely on morphographic characters.

Two species of *Biharisporites* have been described from the Upper Devonian of Canada by Chaloner (1959) and one by McGregor (1960). One of Chaloner's species, *B. ellesmerensis* is within the size range of the *Archaeopteris* megaspores but differs primarily in having considerably larger sculptural elements; McGregor's species *B. submamillaris* is larger (280–610 μ).

Microspores. The equatorially flattened microspores of *Archaeopteris* cf. *jacksoni* are circular to subtriangular in outline. The triradiate mark extends over about two-thirds of the spore radius, in some specimens nearly to the equator, and is formed by a simple suture. The exine is about 2–4 μ thick and is evenly covered with an ornament of small conical elements 1–1.5 μ high and 1 μ or less wide at the base. In some spores an inner membrane (mesosporium?) is present (Pl. 1, fig. 9), but in others it is not seen.

Circular miospores with an ornament of minute conical projections can be referred to the form genus *Cyclogranisporites* Potonié & Kremp (1954). This genus is ubiquitous throughout the Carboniferous, and a Lower Carboniferous form very similar to the microspores of *A.* cf. *jacksoni* has recently been described by Playford (1962) as *Cyclogranisporites lasius*. Chaloner (1963) has recorded the genus in sediments of Lower or Middle Devonian age from Southern England.

It has proved impossible to determine the precise arrangement of the two types of sporangia on the fertile pinnae. However, three adjacent spore-masses belonging to the same pinnule (ringed on Pl. 1, fig. 3) were dissected out and macerated. It was found that two of the spore-masses were composed of microspores and one of megaspores, and it seems therefore, that both microsporangia and megasporangia are borne on the same pinnule in *A.* cf. *jacksoni*.

Each of the spore-masses is enclosed in a coat of acid-resistant cutinised material in the form of globules or as a continuous non-cellular layer adhering to the spores. In some of the spore-masses this residue extends beyond the end of the mass and forms a short protrusion about 60 μ in length which might represent the remains of the sporangium stalk (Pl. 1, fig. 4). The coat of cutinised material is presumably a residue of the same nature as that reported in *Psilophyton* sporangia by Lang (1931) which he terms a "tapetum", in the sporangia of *Archaeopteris latifolia* by Arnold (1939), in the sporangia of *Svalbardia polymorpha* by Høeg (1942), and is probably what Beck (1960) calls non-cellular reticulate thickenings in the sporangia of *Archaeopteris* cf. *macilenta*.

Feller (1953) and Boterberg (1956) have described inclusions associated with the formation of pseudospores during microsporogenesis in *Marsilea* which somewhat resemble the globules of tapetal substance in the sporangia of *Archaeopteris* cf. *jacksoni*. Boterberg believes that in *Marsilea* the pseudospores are formed from the residual mass of plasmodial material which results from a lessening of meiotic activity.

COMPARISON WITH SPORANGIA OF OTHER SPECIES OF *ARCHAEOPTERIS*

Although heterospory has been inferred in several species of *Archaeopteris* (Kräusel & Weyland 1941) it has only hitherto been positively demonstrated in one, *Archaeopteris latifolia*, from the Upper Devonian of Pennsylvania (Arnold 1939). The spore-masses of *A. latifolia* are about as large as those of *A. cf. jacksoni*, and although the diameter of the megaspores in the two is very similar, the number per spore-mass is greater in the Scaumenac species. The microspores in *A. latifolia* are somewhat smaller, being only 35μ in diameter. Beck (1960) has found spores of only one size in the sporangia of *A. cf. macilenta*, but as he later pointed out (Beck 1962) this could mean that the species was dioecious or bore the megasporangia and microsporangia on different leaves or branches.

I have had the opportunity to examine some fertile material of *A. latifolia* from the Port Allegany locality presented to the British Museum (Natural History) by Dr. W. G. Chaloner. Due possibly to a slight difference in preservation this material has given a certain amount of information additional to Arnold's original account.

Arnold (1939) describes only spore-masses from his material of *A. latifolia* and does not give any information about the sporangium wall. In the British Museum material of this species, bulk maceration of the shale results in the release of isolated, incomplete sporangium cuticles the largest measuring 2.5 mm. in length by 0.3 mm. in width, bearing the clear impression of a cellular reticulum (Pl. 2, figs. 4, 5). The cells of the reticulum are isodiametric, measuring about 60–80 μ across, and on certain of the cuticles a somewhat thinner zone of cells runs longitudinally along the length of the sporangium. The cells of this thinner band are more or less elongated, measuring 80 by 60 μ and are uniseriate (Pl. 2, fig. 5). Although no definite dehiscence mechanism has been demonstrated in the sporangia of *Archaeopteris* it has been suggested that spore release was preceded by a simple longitudinal splitting of the sporangium wall (Beck 1960). The longitudinal band of cells in the cuticles of *A. latifolia* would probably facilitate dehiscence of this type by presenting an area of weakness along which splitting could occur.

Tapetal residues in the form of small acid-resistant cutinised globules are also present in the sporangia of *A. latifolia*, and in many forms a thick covering on the inside of the cuticle (Pl. 2, fig. 8).

Adhering to the inside of most of the sporangium cuticles are more or less circular spores 35–50 μ in diameter (Pl. 2, fig. 7). A clear triradiate mark extends between one-half to three-quarters of the spore radius and is formed by a simple suture. The exine is about 1 μ thick and is evenly covered with small conical elements 1 μ high and 1 μ or less broad at the base. The morphology of these spores is essentially the same as that of the microspores of *A. jacksoni* and consequently they could also be referred to the genus *Cyclogranisporites*.

The occurrence of spores inside the sporangium cuticle is too frequent to be the result of chance association, and several spores can be found on some of the larger fragments of cuticle. The lower size limit of these spores corresponds to that given by Arnold for the microspores of *A. latifolia*, but Arnold does not record any sculptural elements on the exines of the microspores he isolated. Beck (1960) has

reported the occurrence of spores, 44–68 μ in diameter, with finely spinose exines in the sporangia of *A. cf. macilenta*. To judge solely from his illustrations of these spores (pl. 27, figs. 8, 9) they appear to be of the *Cyclogranisporites* type. If, as suggested by Beck, his inability to demonstrate heterospory in *A. cf. macilenta* was due to the species being dioecious, or bearing the megasporangia and microsporangia on different branches or leaves, the spores described by him could be the microspores of another heterosporous species of *Archaeopteris*, and this is, as Beck points out, a much more acceptable alternative than to consider the genus as including both homosporous and heterosporous species.

In the material of *A. latifolia* from Port Allegany, none of the sporangium cuticles which I have examined contained megaspores. However, a large number of megaspores was recovered from the maceration residues of the matrix. These megaspores are more or less circular in polar view and 300–400 μ in diameter. The triradiate mark extends from one-half to three-quarters of the spore radius and has lips 7 μ wide. The exine is about 7–8 μ thick with frequent secondary folds. The ornamentation ranges from conical elements in which the length is more than twice the basal diameter (spinae), to raised ridges forming an irregular reticulate sculpture about 5 μ high (muri or cristae). On the contact faces of all these forms the sculptural elements are smaller than those covering the rest of the exine. An inner membrane (mesosporium?) can be seen in some specimens (Pl. 2, fig. 6). The extremes of variation in exine ornamentation in the megaspores makes it impossible to assign them to any one form genus. Those forms with an ornamentation of conical appendages could be included in the megaspore genus *Biharisporites*, and megaspores of essentially this type have been found in the megasporangia of *A. cf. jacksoni*.

The megaspores of *A. latifolia* described by Arnold (1939) are within the size range of the megaspores described here, but no highly developed sculpturing is present on his specimens, the exine being only "slightly roughened". It is possible that the megaspores described above are those of *A. latifolia* and that differences in preservation or in maceration procedure can account for the more pronounced ornamentation in my material. However, because proof of organic connection is lacking this suggestion is at the most very tentative, and is based merely on the association of the spores and sporangia.

DISCUSSION. One of the most interesting facts to emerge from the present study of the sporangia of *Archaeopteris* is the similarity of the spores in the various species. The microspores of *A. cf. jacksoni* and of *A. latifolia* are almost identical and both are referable to the genus *Cyclogranisporites*, and those of *A. cf. macilenta* described by Beck (1960) are clearly similar. In addition, the megaspores of *A. cf. jacksoni* and possibly those of *A. latifolia* are morphologically alike.

That the various species of a plant genus should have spores that are morphologically similar is in no way unusual (see for example the microspores of *Selaginella eggersii* and *Selaginella radiata* figured by Erdtman (1957, text-figs. 177, 180)). However, spores very similar to the microspores of *Archaeopteris* have also been found in some other Devonian plant genera, e.g., *Sporogonites exuberans* Halle from the Lower Devonian of Rörågen in Norway (Halle 1916) and *Svalbardia*

polymorpha from the upper Middle Devonian or lowermost Upper Devonian of Spitsbergen (Høeg 1942) and would therefore be of limited taxonomic value.

IV CONCLUSIONS

The present study of the fructification of *Archaeopteris* cf. *jacksoni* in which the microsporangia and megasporangia are in organic connection further demonstrates heterospory in this genus and supports Beck's and Kräusel & Weyland's supposition that, in all probability, all *Archaeopteris* is heterosporous.

The occurrence of both microspores and megaspores in the sporangia of *Barinophyton richardsoni* demonstrates that the genus is definitely heterosporous and is the more noteworthy for being so, as it differs conspicuously from other Devonian heterosporous plants.

It would seem that heterospory in the Upper Devonian appeared independently in more than one line of plants, and it has already been shown (Chaloner & Pettitt 1963, 1964) that at least one group had by that time reached a level of heterospory that is the hallmark of the seed.

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PLATE 1

Archaeopteris cf. jacksoni (Dawson)

Upper Devonian ; Scaumenac Bay, Quebec

FIG. 1. Part of a fertile primary pinna bearing 18 or 19 pinnae, $\times \frac{1}{2}$. V.44711.

FIGS. 2, 3. Fertile pinnae from which spore-masses were dissected out. The ring (Fig. 3) surrounds two microsporangia and one megasporangium on the same pinnule. Fig. 2 $\times 1$. Fig. 3, $\times 2$. V.51316, V.51312.

FIG. 4. Small megaspore-mass with a cutinised basal projection, $\times 50$. V.51326.

FIG. 5. Microspore-mass, $\times 50$. V.51327.

FIG. 6. Megaspore-mass, $\times 50$. V.51327.

FIG. 9. Microspore separated from microspore-mass, $\times 500$. V.51316.

Barinophyton richardsoni (Dawson)

Upper Devonian ; Perry, Maine

FIGS. 7, 8. Specimens from which spores were isolated (part and counterpart), $\times 1$. V.51350, V.51351.

FIG. 10. Microspore, $\times 500$. V.51357.

Figs. 1-3, 7, 8 were photographed under xylol.

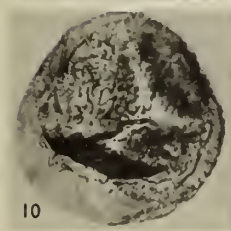
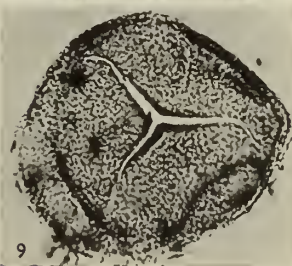
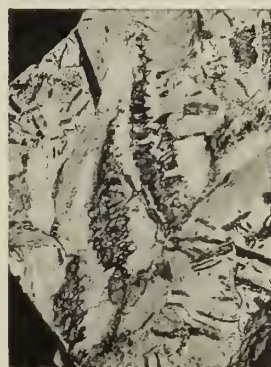
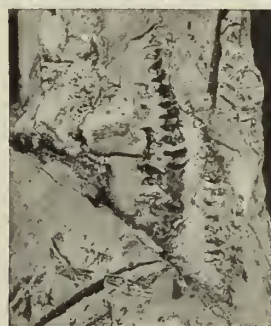
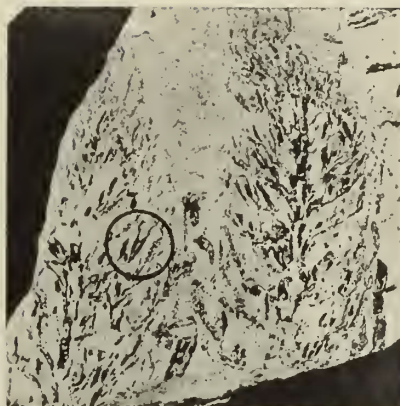
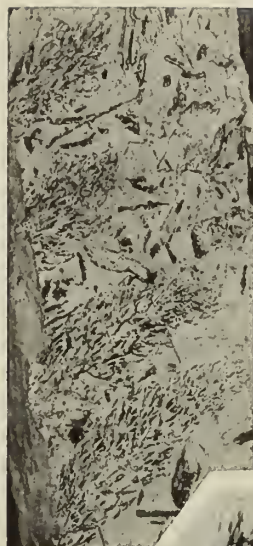


PLATE 2

FIG. 1. *Archaeopteris* cf. *jacksoni* (Dawson). Megaspore, $\times 200$. V.51325.

FIG. 2. *Barinophyton richardsoni* (Dawson). Megaspore, $\times 200$. V.51357.

Archaeopteris latifolia Arnold

Upper Devonian ; Pennsylvania.

FIGS. 3, 6. Megaspores recovered from maceration residues of matrix, $\times 200$. V.51311, V.51310.

FIGS. 4, 5. Incomplete sporangium cuticles showing a clear cellular reticulum. A thinner longitudinal zone is seen towards the right in Fig. 5. The circular objects are microspores. The background has been painted out. $\times 50$. V.51302, V.51303.

FIG. 7. Microspore inside sporangium cuticle, $\times 500$. V.51303.

FIG. 8. Sporangium cuticle with adherent tapetal globules, $\times 450$. V.51303.

